Characterisation of large zooplankton sampled with two different gears during midwinter in Rijpfjorden, Svalbard

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Abstract: During a midwinter cruise north of 80ºN to Rijpfjorden, Svalbard, the composition and vertical distribution of the zooplankton community were studied using two different samplers 1) a vertically hauled multiple plankton sampler (MPS; mouth area 0.25 m², mesh size 200 μm) and 2) a horizontally towed Methot Isaacs Kidd trawl (MIK; mouth area 3.14 m², mesh size 1500 μm). Our results revealed substantially higher species diversity (49 taxa) than if a single sampler (MPS: 38 taxa, MIK: 28) had been used. The youngest stage present (CIII) of *Calanus* spp. (including *C. finmarchicus* and *C. glacialis*) was sampled exclusively by the MPS, and the frequency of CIV copepodites in MPS was double that than in MIK samples. In contrast, catches of the CV-CVI copepodites of *Calanus* spp. were substantially higher in the MIK samples (3-fold and 5-fold higher for adult males and females, respectively). The MIK sampling clearly showed that the highest abundances of all three *Thysanoessa* spp. were in the upper layers, although there was a tendency for the larger-sized euphausiids to occur deeper. Consistent patterns for the vertical distributions of the large zooplankters (*e.g.* ctenophores, euphausiids) collected by the MPS and MIK samplers provided more complete data on their abundances and sizes than obtained by the single net. Possible

mechanisms contributing to the observed patterns of distribution, *e.g.* high abundances of both *Calanus* spp. and their predators (ctenophores and chaetognaths) in the upper water layers during midwinter are discussed.

Introduction

In pelagic ecosystems zooplankton is the key link between primary producers and the higher trophic levels. Zooplankters play an integral role in the recycling of nutrients and dissolved organic matter within the water column. Zooplankton is normally patchily distributed across a broad range of horizontal spatial scales from the micro scales (<10 m) of copepod patches (*e.g.* Trudnowska *et al.* 2016) to much larger scales as seen in some of the dense swarms (10 m to 1 km) of euphausiids (Folt and Burns 1999; Lough and Broughton 2007). Vertical distributions are also finely structured and the need to quantify these 3-D patterns has encouraged development of sampling gears that can properly quantify zooplankton abundance and community structure (Wiebe *et al.* 2002). The development of multiple net sampling systems, designed to discriminate discrete depth strata, has improved the precision with which we can determine the abundance and depth distribution of zooplankton (see review by Wiebe and Benfield 2003). The choice of mesh size and net type is a basic consideration with regard to achieving appropriate sampling efficiency (Pearcy *et al.* 1983). Many studies (*e.g.*, Vannucci 1968; Antacli *et al.* 2010 and citations therein) have shown that no single net system or mesh size can adequately sample the complete spectrum of plankton sizes. In order to achieve more representative estimates of abundance across a broader range of size spectrum of zooplankton, a combination of different nets needs to be used and the size-related sampling efficiency of each net taken into account when analysing and interpreting the data.

Using only standard mesozooplankton gear such as MPS or WP2 nets leads to substantial underestimation of both tiny specimens (Gallienne and Robins 2001; Hopcroft *et al.* 2005) as well as the larger zooplankters (*e.g.* Vinogradov 1997; Sameoto *et al.* 2000). The key factors that affect the precision of samples include: diel vertical migration, sensory perception by the target species (noise, vision, pressure wakes), swimming capabilities of young versus mature individuals, and their feeding behaviours (Johnson and Fogarty 2013). For example, avoidance and detection of nets disproportionally affects abundance estimates of the larger and faster swimming zooplankters, which cannot only be a numerically significant part of the community, but also occupying key positions in food webs (*e.g.* carnivores that are sparsely distributed). The problem is even more acute when

trying to estimate most ctenophores and siphonophores because they are almost impossible to be sampled quantitatively. Predators are expected to occur in lower abundances than their prey, and often not only are their distributions patchy, both vertically and horizontally (Swanberg and Båmstedt 1991). Moreover, the problem of trying to comprehend three-dimensional distributions with the fourth dimension of time with a one-dimensional linear sampling is yet to be resolved but using arrays of samplers with different characteristics can improve our insights.

In this study we present data collected during a cruise to the ice free area north of 80°N in January 2012, which aimed to describe the differences in species composition, vertical distributions and size spectra of the zooplankton communities sampled using two different gears; 1) a vertically hauled multiple plankton sampler (MPS) with a mouth area of 0.25 m² and mesh size of 200 μm and 2) a horizontally towed modified Methot Isaacs Kidd trawl (MIK) with a mouth area of 3.14 m² and mesh size of 1500 μm. Although there have been a few recent investigations of the mesozooplankton communities in the European Arctic during wintertime (*e.g*. Daase *et al*. 2014; Grigor *et al*. 2014; Båtnes *et al*. 2015; Błachowiak-Samołyk *et al*. 2015; Lischka and Hagen 2016) and some macrozooplankton (*e.g*., Søreide *et al*. 2003; Zhukova *et al*. 2009; Webster *et al*. 2015; Grenvald *et al*. 2016; Bandara *et al*. 2016) more comprehensive data on a broader spectrum of zooplankton size fractions is needed if our current level of understanding continues to be based solely on data for the more abundant and readily sampled size fractions (*e.g*. mesozooplankton).

The aims of this paper are threefold: 1) to describe differences in the diversity, vertical distributions and sizes of the zooplankton derived from two different nets; 2) to demonstrate the effectiveness of the two gears (MPS and MIK) in sampling *Calanus* population, and 3) to contribute to expand our poor knowledge of large zooplankters such as euphausiids, gelatinous organisms and chaetognaths, which generally occur at relatively low densities.

Material and methods

Study area. — This study was a component of the Polar Night Cruise conducted in January 2012 by R/V *Helmer Hanssen* in Rijpfjorden, an Arctic fjord on the most northern island of Spitsbergen, Nordaustlandet (Fig. 1). The multiple plankton sampler (MPS) samples were collected on 12 January 2012 at an inner station (MPS 1, 80° 18.51 N, 22° 15.70 E) and on 13 January 2012 at an outer Rijpfjorden station (MPS 2, 80° 18.75 N, 22° 15.98 E), ~30 km apart. The MIK samples were collected near the outer MPS 2 station (Fig. 1; Tables 1 and 2). Rijpfjorden is a north-facing fjord (max. 270 m deep), with a wide opening towards the broad shallow shelf (100–200 m deep), connecting

Fig. 1. Sampling region in northern Svalbard waters. MPS 1 (inner) and MPS 2 (outer) stations
marked as red dots. MIK sampling site was marked as a circle near MPS 2 station.

it to the Arctic Ocean. Generally the hydrography of the fjord is dominated by
cold Arctic water masses, since inflows of Atlantic water are far less pronounced
than into the fjords along the western coast of Spitsbergen. Since the advection
of relatively warm Atlantic water into the fjord during the ice-covered period is
so limited, the zooplankton community is dominated by Arctic species (Falk-
-Petersen *et al*. 2008). However, episodic inflows of Atlantic water may occur
from the West Spitsbergen Current during the ice-free period in autumn, which
may introduce zooplankton and fish of Atlantic origin into the fjord. In January
2012 the waters of Rijpfjorden were homogenous with cold and a low salinity
waters at the surface, separated from the deeper, slightly warmer water by
a sharp pycnocline at 60–70 m depth (Falk-Petersen *et al*. 2014). The fjord was
ice free, except the fast ice from land that was in the inner part of the fjord.

Table 1

Overview of Multinet (MPS) zooplankton samples taken from standard depth layers (0-20-50-100-200-260 m) from the R/V *Helmer Hanssen* from two stations inner (MPS 1) during midday and outer (MPS 2) during midnight situated in Rijpfjorden (see Fig. 1 for details) during the Polar Night Cruise of January 2012.

MPS	Date	Time (UTC)	Depth layer (m)	Latitude	Longitude
MPS 1_1	12.01.2012	13:10	260–200	80°18.51 N	22°15.70 E
MPS 1_2	12.01.2012	13:10	200–100	80°18.51 N	22°15.70 E
MPS 1_3	12.01.2012	13:10	100–50	80°18.51 N	22°15.70 E
MPS 1_4	12.01.2012	13:10	50–20	80°18.51 N	22°15.70 E
MPS 1_5	12.01.2012	13:10	20–0	80°18.51 N	22°15.70 E
MPS 2_1	13.01.2012	01:05	260–200	80°18.75 N	22°15.98 E
MPS 2_2	13.01.2012	01:05	200–100	80°18.75 N	22°15.98 E
MPS 2_3	13.01.2012	01:05	100–50	80°18.75 N	22°15.98 E
MPS 2_4	13.01.2012	01:05	50–20	80°18.75 N	22°15.98 E
MPS 2_5	13.01.2012	01:05	20–0	80°18.75 N	22°15.98 E

Table 2

Overview of MIK nets horizontally towed at standard depth layers (20, 75 and 225 m) from the R/V *Helmer Hanssen* in Rijpfjorden (see Fig. 1 for details) during the Polar Night Cruise of January 2012.

MIK	Date	Time (UTC)	Depth (m)		Latitude	Longitude
MIK 1	12.01.2012	11:46	75	Start	80°19.09 N	22°11.39 E
				End	80°19.17 N	22°11.45 E
MIK 2	12.01.2012	12:22	225	Start	80°18.86 N	22°14.75 E
				End	80°18.59 N	22°16.14 E
MIK 3	13.01.2012	23:53	20	Start	80°18.51 N	22°15.96 E
				End	80°18.73 N	22°18.13 E
MIK 4	13.01.2012	00:29	75	Start	80°18.76 N	22°15.99 E
				End	80°19.27 N	22°15.08 E
MIK 5	13.01.2012	11:04	20	Start	80°18.79 N	22°14.4 E
				End	80°19.10 N	22°14.46 E
MIK 6	13.01.2012	11:36	75	Start	80°19.10 N	22°14.48 E
				End	80°19.10 N	22°17.01 E
MIK 7	13.01.2012	12:18	225	Start	80°18.61 N	22°15.36 E
				End	80°18.24 N	22°14.69 E

Net sampling. — MPS sampling was conducted using a standard multiple plankton sampler (MPS, Hydro-Bios Kiel), consisting of five opening/closing nets, each with 0.25 m² mouth opening and 200 μm mesh size. Two vertical hauls at a speed of 40 m min⁻¹ were carried out at the Rijpfjorden stations at midday and midnight sampling, but there was no indication of any diel vertical migration occurring (data not shown). The MPS net was lowered up to approx. 10 m above the bottom and then hauled back to the surface to provide an integrated sample from five following depth layers: 0–20, 20–50, 50–100, 100–200 and 200–260 m (Table 1).

The MIK assemblage was sampled using an open Methot Isaacs Kidd trawl modified as a ring net with a mouth opening of 3.15 m² (ICES 2013). The net was 12 m long, with a mesh size of 1500 μm, which reduced to 500 μm mesh net in the last meter and a 10-L cod end. The net was trawled for 10 min at a speed of ~1.5 knots (0.75 m s⁻¹) at three depth horizons (20, 75 and 225 m) in Rijpfjorden with separate horizontal tows at each depth. A total of seven MIK casts were achieved at both midday and midnight (Table 2). Tow depth was controlled using the live feed from a Simrad PI depth sensor. After net recovery, the cod end was transferred immediately to a bucket and diluted up to the 9-L mark in the laboratory on board. Subsamples of 0.6 L were then taken after gentle mixing.

Neither net was fitted with a flowmeter mounted on both nets, so volumes of water filtered were estimated based on net opening, depth layer, towing speed and time assuming that MIK net's trajectory was horizontal. The volume of water sampled by MPS ranged from 5 m³ to 25 m³, while it was much higher for horizontally towed MIK net amounting from 1099 m³ up to 8723 m³. The exception was one day MIK haul from 75 m (where lots of ice in the surface water column appeared), in which the volume of seawater filtered amounted to 345 m³.

All zooplankton samples were preserved in 4% hexamethylenetetramin-buffered formaldehyde directly after collection. Zooplankton taxa were identified and counted under a stereomicroscope equipped with an ocular micrometer, according to the standard procedures described by Harris *et al.* (2000). Small-sized zooplankton below 5 mm (Copepoda except CIV and older copepodites stages of *Calanus hyperboreus*, juvenile stages of Pteropoda, Euphausiacea, Ostracoda, Amphipoda and Chaetognatha) were identified and counted in sub-samples obtained from a fixed sample volume by automatic pipette (approximately 500 individuals). All large zooplankton taxa (older than CIV stages of *C. hyperboreus*, advanced developmental stages of Pteropoda, Euphausiacea, Amphipoda, Decapoda, Appendicularia, Chaetognatha and larval stages of Pisces) were sorted, identified and measured from the whole sample. At least ten first individuals from each large zooplankton taxon were measured in each sample. In case of longitudinal shape zooplankton (Euphausiacea, Amphipoda, Decapoda, Appendicularia), as a total length, distance from the top of a head/ tip of a rostrum to the end of the body was used (*e.g.* Søreide *et al.* 2003). In case of round shape zooplankton species (*e.g.* pteropod *Limacina helicina*), the

diameter was used as an equivalent for total length (Gannefors *et al*. 2005). All representatives of *Calanus* spp. were identified to species level based on morphology and prosome lengths of individual copepodite stages (*cf*. Tande 1991; Kwaśniewski *et al*. 2003).

Previously, Webster *et al*. (2015) published the MIK data from the same cruise, along with multifrequency acoustics, to describe the vertical distribution of macrozooplankton biomass over a diel cycle, while MPS data have been presented for biomass comparison of protist and mesozooplankton in two contrasting locations: a shallow Rijpfjorden and a deep ice-covered region of Sofiadjupet (Błachowiak-Samołyk *et al*. 2015).

Data analyses. — The abundance data for the different developmental stages of the dominant copepod species and other zooplankton were converted to the number of individuals in 1 m^3 and displayed graphically. There were no statistically significant differences between day and night abundances and sizes (data not shown) within either the MPS or the MIK samples, so the values from each sampling stratum were averaged separately for the MPS (0–20 m, 20–50 m, 50–100 m, 100–200 m and 200–260 m) and MIK (20 m, 75 m and 225 m). It was confirmed by our data that two MPS sampling stations located ~30 km apart were similar concerning bottom depth, water masses distribution and assemblages of zooplankton, so we decided to present obtained results as mean zooplankton abundances from both MPS 1 and MPS 2 stations following the pattern published in Błachowiak-Samołyk *et al*. (2015).

We used a similarity percentages analysis (SIMPER) to assess which species discriminated between the data from the two samplers. This analysis was run using PRIMER version 6.0 (Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Warwick 1994).

All appropriate *Calanus finmarchicus* and *C*. *glacialis* copepodite stages were combined into *Calanus* spp. category when their patterns in vertical distribution were analysed (Fig. 5).

The size data for the individual taxa, which had a constant variance and were normally distributed, were examined by a standard t-test with the software STATISTICA v.9.1 (StatSoft, Inc. 2010). Additionally, a Spearman rank test was employed to test for any correlation between zooplankton size and frequency in MPS and MIK samples.

Results

MPS and MIK community structures. — A total of 49 taxa were sampled by the two nets. Of these 22 were exclusive to the MPS samples and 11 to the MIK samples, so only 16 taxa were sampled by both gears (Table 3). The copepods

Oithona similis and *Pseudocalanus* spp. contributed 33% and 30% respectively to the total zooplankton abundances in the MPS samples, and *Calanus finmarchicus* and *C. glacialis* contributed 16% and 6%, respectively. In contrast, *C. finmarchicus* and *C. glacialis* were numerically dominant in the MIK samples, contributing 51% and 28%, respectively, to the total zooplankton abundance. *Metridia longa* (11%) and *C. hyperboreus* (6%) were third and fourth in overall zooplankton abundance in MIK samples. The 16 taxa common to both sets of samples included the older stages (> CIII) of *Calanus* spp., larger copepod species (*Paraeuchaeta* spp. and *Bradyidius similis*), chaetognaths (predominantly *Parasagitta elegans*), euphausiids (*Thysanoessa longicaudata*), gelatinous zooplankton (the ctenophores *Beröe cucumis* and *Mertensia ovum*) and other zooplankters (highlighted in grey in Table 3). Species exclusively sampled by the MPS included the smaller sizes of copepod (*e.g.* different development stages of *O. similis*, *Triconia borealis*, *Microcalanus* spp., *Pseudocalanus* spp.), young stages of *Calanus* spp. (CIII), young stages of pteropods (*Clione limacina* and *Limacina helicina*), appendicularians (*Oikopleura* spp. and *Fritillaria borealis*) and smaller gelatinous zooplankton (*Aglantha digitale* ≤5 mm, Ctenophora larvae and Hydrozoa). In the MIK net samples, large zooplankters, such as larval stages of polychaetes, older stages of pteropods (*C. limacina*), euphausiids, amphipods and larger gelatinous animals (hydromedusa *A. digitale* >5 mm) (Table 3) were abundant.

The SIMPER analysis revealed that average dissimilarities in zooplankton community composition between MPS and MIK net samples was around 67%. *Oithona similis* was the species contributing most (10%) to difference between the data for the MPS and MIK samples. Other small and abundant taxa in the MPS samples included *Pseudocalanus* spp. (with 6–7% contribution to dissimilarity of copepodite stages from CI to CV), adults *T. borealis* (with 6% contribution), *Microcalanus* spp. (5%), *C. finmarchicus* CIV (3%), small (< 5 mm) specimens of *Oikopleura* spp. (3%) and adult males of *M. longa* (3%) contributed to the dissimilarity between the two sets of samples.

Table 3

Frequency of all identified zooplankton taxa/species/stages found in MPS and MIK together with average abundance, separately in MPS and MIK and their contribution to dissimilarity (SIMPER). The common MPS and MIK group present in both net types are highlighted by grey.

Taxon	Frequency of all taxa identified in		Average abundance (ind.m^{-3}) in		Contribu- tion to dissimilarity
	MPS	MIK	MPS	MIK	
Acartia longiremis (Lilljeborg, 1853) CI-CVI	100	0	0.06	0	0.08
Aetideidae CI-CIII	100	0	1.18	0	1.96
Aglantha digitale (O.F. Müller, 1776) = <5 mm	100	0	0.01	0	0.02
Bivalvia veliger	100	0	0.09	0	0.15
Calanus finmarchicus (Gunnerus, 1770) CIII	100	0	0.75	0	1.28
Calanus glacialis Jaschnov, 1955 CIII	100	0	0.98	0	1.57
Calanus hyperboreus Krøyer, 1838 CIII	100	0	0.11	0	0.19
Clione limacina (Phipps, 1774) <5 mm	100	0	0.04	0	0.06
Copepoda nauplii	100	0	0.3	0	0.59
Ctenophora larvae	100	0	0.42	0	0.65
Cyclocaris guilelmi Chevreux, 1899	100	0	0.01	0	0.01
Echinodermata larvae	100	0	0.1	0	0.17
Fritillaria borealis Lohmann, 1896	100	0	0.12	0	0.19
Gastropoda veliger	100	0	0.24	0	0.37
Harpacticoida indet.	100	0	0.15	0	0.27
Hydrozoa medusae indet.	100	0	0.09	0	0.14
Isopoda *Bopyridae*	100	0	0.47	0	0.76
Limacina helicina (Phipps, 1774) <5 mm	100	0	1	0	1.7
Metridia longa (Lubbock, 1854) CI–CIV	100	0	0.32	0	0.52
Microcalanus spp.	100	0	2.76	0	4.75
Oikopleura spp. <5 mm	100	0	1.63	0	2.75
Oithona atlantica Farran, 1908	100	0	1.17	0	1.92
Oithona similis Claus, 1866	100	0	5.25	0	9.14
Ostracoda	100	0	0.02	0	0.03
Pseudocalanus minutus (Krøyer, 1845) AF	100	0	0.56	0	0.96
Pseudocalanus spp. CI–CV	100	0	2.44	0	4.19
Pseudocalanus spp. AM	100	0	0.13	0	0.23
Pseudomma truncatum S.I. Smith, 1879	100	0	0.02	0	0.03

Table 3 – continued

Taxon	Frequency of all taxa identified in		Average abundance (ind.m⁻³) in		Contribution to dissimilarity
	MPS	MIK	MPS	MIK	
Triconia borealis (G.O. Sars, 1918)	100	0	1.68	0	2.88
Travisiopsis spp.	100	0	0.16	0	0.28
Beroe cucumis Fabricius, 1780	98	2	1.19	0.11	1.87
Mertensia ovum (Fabricius, 1780)	91	9	0.05	0.01	0.08
Calanus hyperboreus Krøyer, 1838 CIV	73	27	1.16	0.71	1.69
Bradyidius similis (G.O. Sars, 1902) CIV–CVI	71	29	0.13	0.07	0.3
Calanus glacialis Jaschnov, 1955 CIV	71	29	2.81	2.13	2.28
Paraeuchaeta spp. CV	69	31	0.02	0.01	0.05
Calanus finmarchicus (Gunnerus, 1770) CIV	69	31	3.61	2.49	3.26
Calanus finmarchicus (Gunnerus, 1770) CV	54	46	4.04	3.66	2.18
Calanus glacialis Jaschnov, 1955 AM	47	53	1.17	1.54	1.33
Parasagitta elegans (Verrill, 1873) => 10 mm	42	58	0.16	0.3	0.4
Paraeuchaeta norvegica (Boeck, 1872) AF	41	59	0.01	0.02	0.04
Calanus glacialis Jaschnov, 1955 CV	41	59	2.27	2.56	2.11
Calanus hyperboreus Krøyer, 1838 AM	35	65	0.1	0.25	0.42
Apherusa glacialis (Hansen, 1888)	32	68	0.01	0.04	0.07
Metridia longa (Lubbock, 1854) AF	30	70	0.89	1.54	1.93
Metridia longa (Lubbock, 1854) CV	28	72	0.92	1.2	2.08
Eukrohnia hamata (Möbius, 1875) => 10 mm	24	76	0.2	0.65	0.86
Thysanoessa longicaudata (Krøyer, 1846)	24	76	0.05	0.21	0.29
Calanus finmarchicus (Gunnerus, 1770) AF	22	78	0.96	1.92	2.24
Calanus glacialis Jaschnov, 1955 AF	18	82	1.47	2.67	2.4
Parasagitta elegans (Verrill, 1873) => 20 mm	17	83	0.57	1.55	1.83
Metridia longa (Lubbock, 1854) AM	14	86	0.87	2.15	2.59
Eukrohnia hamata (Möbius, 1875) => 20 mm	11	89	0.03	0.26	0.38
Calanus hyperboreus Krøyer, 1838 CV	7	93	0.23	1.71	2.45
Calanus finmarchicus (Gunnerus, 1770) AM	5	95	0.2	1.65	2.34
Calanus hyperboreus Krøyer, 1838 AF	4	96	0.13	1.52	2.21
Aglantha digitale (O.F. Müller, 1776) >5 mm	0	100	0	0.4	0.58
Appendicularia larvae	0	100	0	0.008	0
Caligus spp.	0	100	0	0.004	0

Taxon	Frequency of all taxa identified in		Average abundance (ind.m^{-3}) in		Contribution to dissimilarity
	MPS	MIK	MPS	MIK	
Clione limacina (Phipps, 1774) => 5mm	0	100	0.45	0.06	0.72
Erythrops erythrophthalmus (Goës, 1864)	0	100	0	0.003	0
Gaetanus tenuispinus (G.O. Sars, 1900) CIV–VI	0	100	0	0.006	0
Hyperia galba (Montagu, 1815)	0	100	0	0.004	0
Hyperoche medusarum (Krøyer, 1838)	0	100	0	0.02	0.03
Limacina helicina (Phipps, 1774) => 5 mm	0	100	0	0.16	0.3
Paraeuchaeta spp. AM	0	100	0	0.01	0.03
Polychaete larvae	0	100	0	0.07	0.14
Thysanoessa raschii (M. Sars, 1864)	0	100	0	0.04	0.05
Themisto libellula (Lichtenstein in Mandt, 1822) => 5mm	0	100	0	0.05	0.06
Themisto abyssorum (Boeck, 1871) => 5mm	0	100	0	0.07	0.1
Thysanoessa inermis (Krøyer, 1846)	0	100	0	0.16	0.24

Vertical distribution patterns in abundance of larger zooplankton. — There was a consistent pattern in the vertical distribution of gelatinous zooplankters in the two nets. *Mertensia ovum* peaked numerically at 50–100 m in the MPS samples and at 75 m in MIK samples (Fig. 2a). *Beröe cucumis* was caught in higher abundances in MPS samples (maximum 10.3 ind. m^{-3}) than in MIK samples (0.22 ind. m^{-3}) but the peak abundances were found in the upper water layers in both nets (Fig. 2b).

Both chaetognaths, *Parasagitta elegans* and *Eukrohnia hamata*, were sampled in the greatest numbers in the surface layer (0–20 m) in MPS. However, their abundance was four times greater in the MIK at 75 m depth (Figs. 3a–b). The only euphausiid species sampled by both nets was *Thysanoessa longicaudata*, which was most abundant (0.16 ind. m^{-3}) in the deepest layer (200–260 m) sampled by the MPS but was almost two times higher (0.3 ind. m^{-3}) at a shallower layer (75 m) in MIK samples (Fig. 4a). Two other euphausiid species, *T. inermis* and *T. raschii*, both occurred at their highest abundances in the upper water layers sampled by the MIK (Fig. 4b–c).

Copepodites CIV (Fig. 5a) and CV (Fig. 5b) of *Calanus* spp. (combined appropriate stages of *Calanus finmarchicus* and *C. glacialis*) were dominant in the upper 20 m layer in MPS samples (176 and 178 ind. m^{-3}, respectively), while at 75 m in MIK samples (60 and 155 ind. m^{-3}, respectively). There was a similar vertical distribution pattern in adults *Calanus* spp., which maximum
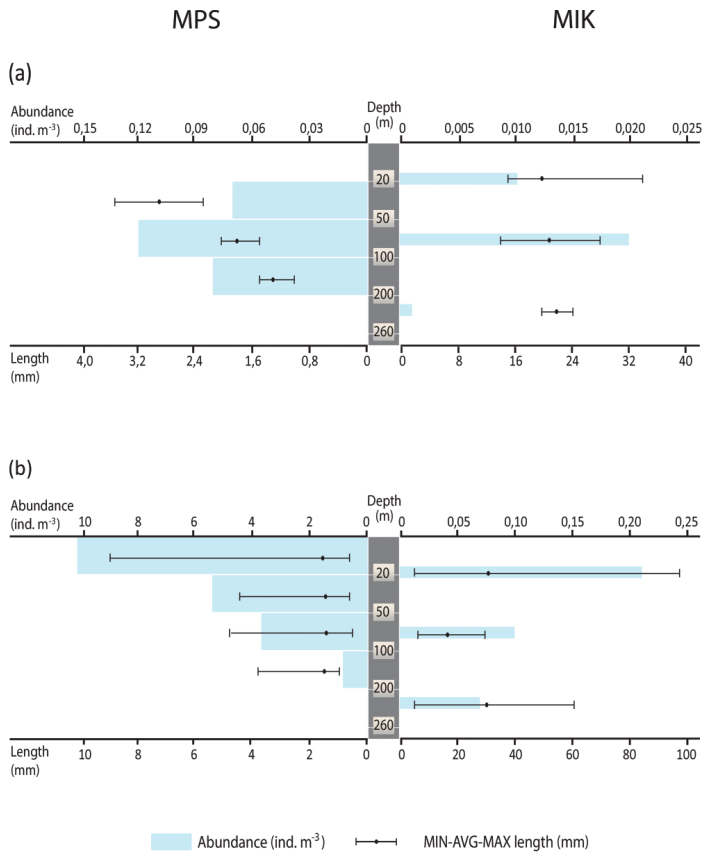
Fig. 2. Vertical distribution patterns of larger zooplankton taxa abundances (ind. m^{-3}) and lengths (mm) in MPS (left panel) and MIK (right panel): a) *Mertensia ovum*; b) *Beröe cumis*. Note scale differences.

concentrations were in the surface layer in both samplers with a peak of females and males in the MIK samples (50 and 13 ind. m^{-3}, respectively) (Figs 5c–d).

Concerning *Calanus hyperboreus* vertical distribution, CIV and CV copepodites were the most abundant stages (6.7 ind. m^{-3}) at 200–260 m in the MPS samples and at 75 m (15.1 ind. m^{-3}) in the MIK samples, respectively (data not shown).

After including all development stages (also CIII present exclusively in MPS samples) of *Calanus* spp. (combined *Calanus finmarchicus* and *C. glacialis*) from the integrated water column a consistent pattern of frequency of particular copepodites stages was obtained (Fig. 6a). Shares of the youngest CIII and CIV stages were the highest in MPS samples (3% and 43%, respectively) while CV and adult females/males prevailed in MIK samples (53% and 20%/6%, respectively) (Fig. 6a). Similar consistency appeared when the frequency of
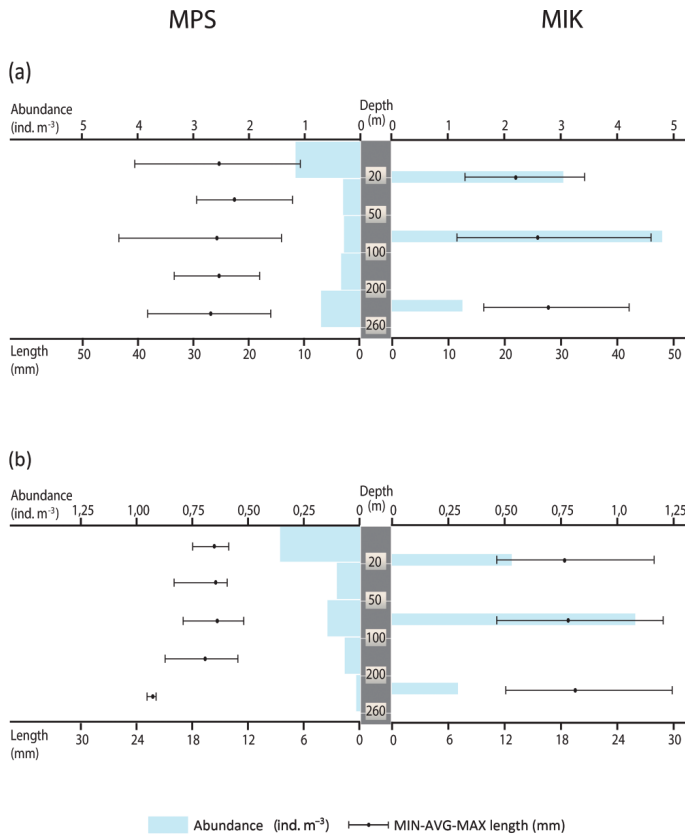
Fig. 3. Vertical distribution patterns of larger zooplankton taxa abundances (ind. m^{-3}) and lengths (mm) in MPS (left panel) and MIK (right panel): a) *Parasagitta elegans* and b) *Eukrohnia hamata*. Note scale differences.

C. hyperboreus stages from the integrated water column was compared between the two nets. Dominant copepodite was CIV in MPS (79%), but CV in MIK (55%) (Fig. 6b). Moreover, the share of females in MIK samples was almost 10-folds higher than in MPS samples (Fig. 6b).

Vertical distribution patterns in size of larger zooplankton. — A Spearman rank correlation (r_s=0.72, p<0.001) between zooplankton size and frequency of occurrence showed that significantly more large individuals were collected by the MIK than the MPS net. The detailed vertical size patterns are described on figures 3–4. The ctenophores *Mertensia ovum* (Fig. 2a) and *Beröe cucumis* (Fig. 2b) showed large variability in their body lengths between the different depths in both nets. Specimens of *Parasagitta elegans* (Fig. 3a) and *Eukrohnia hamata* (Fig. 3b) were generally larger in deeper waters. Also *Thysanoessa*
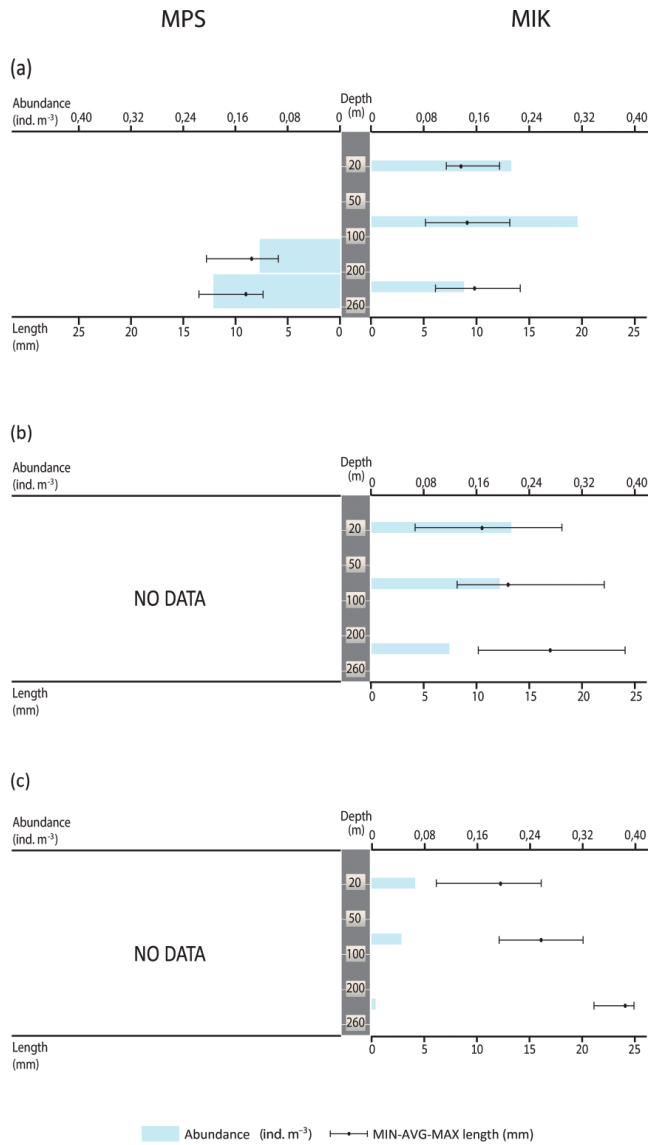
Fig. 4. Vertical distribution patterns of larger zooplankton taxa abundances (ind. m⁻³) and lengths (mm) in MPS (left panel) and MIK (right panel): a) *Thysanoessa longicaudata*; b) *Thysanoessa inermis* and c) *Thysanoessa raschii*.
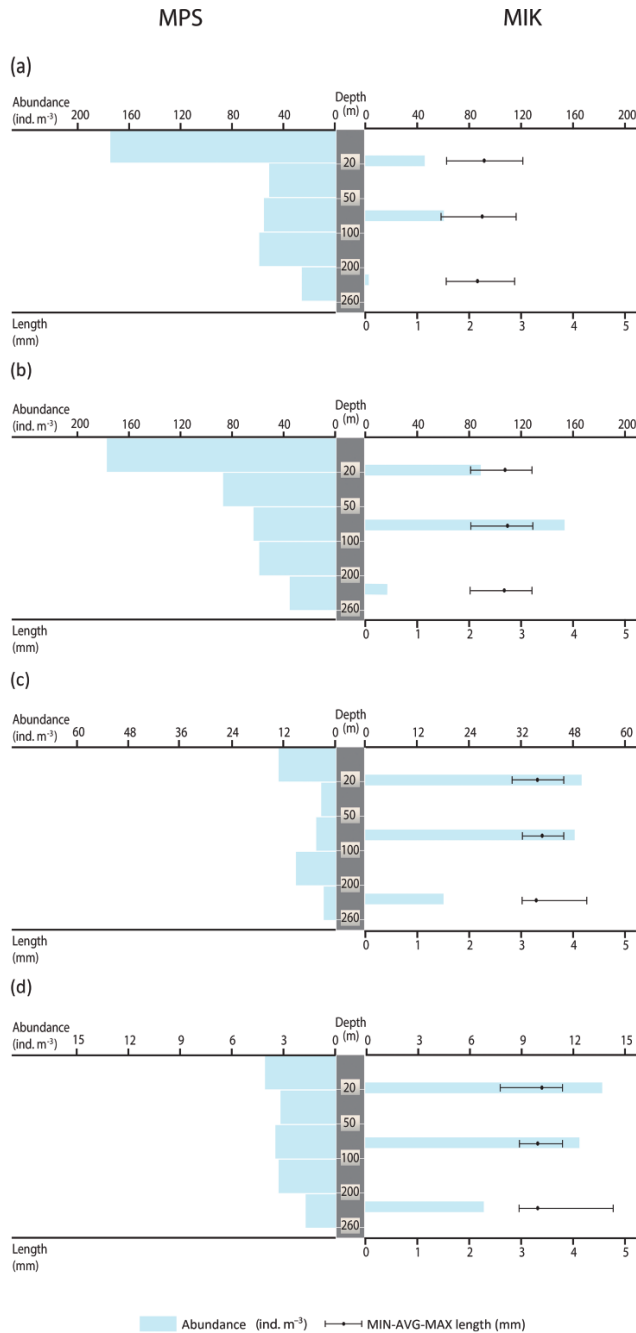
Fig. 5. Vertical distribution patterns of older copepodite stages of *Calanus* spp. (pooled both *C. finmarchicus* and *C. glacialis*) abundances (ind. m^{-3}) in MPS (left panel) and MIK (right panel): a) copepodite stage IV (CIV); b) copepodite stage V (CV); c) copepodite stage VI – adult females (AF) and d) copepodite stage VI – adult males (AM). Note scale differences.
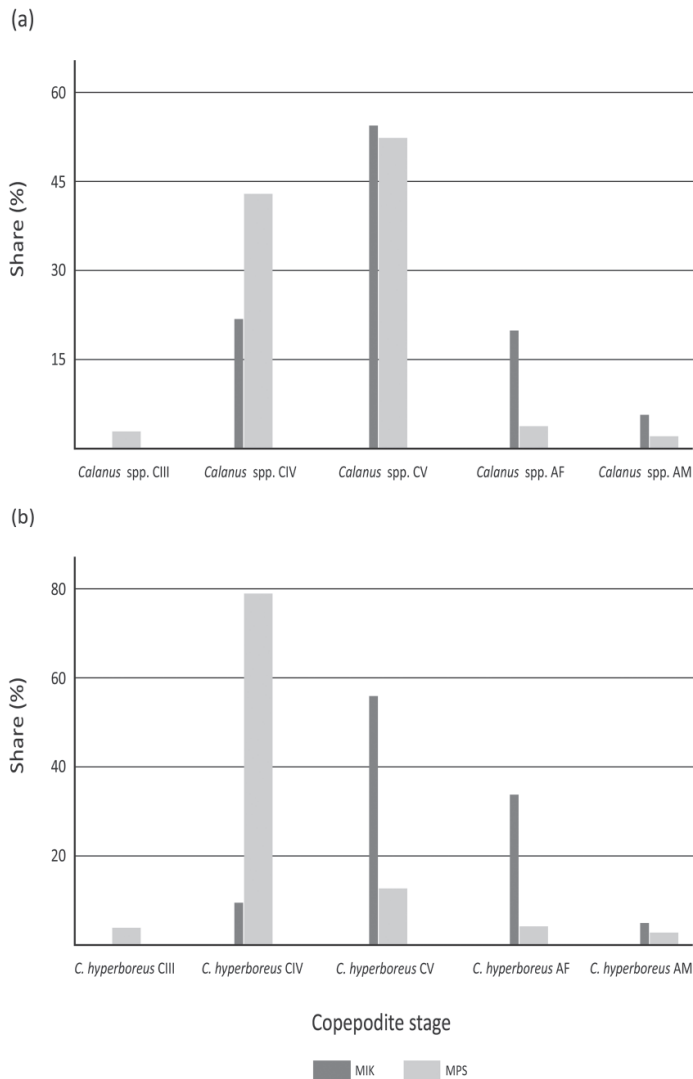
(a)

(b)

Fig. 6. Shares (%) of particular copepodite stages of: a) *Calanus* spp. (including *C. finmarchicus* and *C. glacialis*); b) *C. hyperboreus* integrated from all sampling layers from both gears (MPS and MIK).

longicaudata were larger in the deep layers (Fig. 4a), like the *T. inermis* and *T. raschii*, which were caught exclusively by MIK net (Fig. 4b–c).

Although there were consistent patterns of vertical variability within lengths of all stages of three *Calanus* we included only the results from MIK in Fig. 5. The MPS measurements, which were provided according to classification to the species level based on prosome lengths ranges of individual copepodites stages of all *Calanus* spp. (Kwaśniewski *et al*. 2003), are displayed in Table 4.

Table 4

The results of measurements of prosome lengths and widths (µm)
of three *Calanus* species found in our zooplankton samples.

Calanus development stage	Average prosome (µm)		Number of ind. measured
	length	width	
C. finmarchicus CIV	1997	524	49
C. finmarchicus CV	2509	685	71
C. finmarchicus CVI, AF	3002	796	80
C. finmarchicus CVI, AM	3100	801	38
C. glacialis CIV	2551	668	45
C. glacialis CV	3157	**1029**	57
C. glacialis CVI, AF	3573	**1126**	70
C. glacialis CVI, AM	3602	**1143**	44
C. hyperboreus CIV	3603	**1056**	81
C. hyperboreus CV	4890	**1486**	90
C. hyperboreus CVI, AM	6458	**1487**	78
C. hyperboreus CVI, AM	6220	**1400**	19

Discussion

This study revealed that a relatively diverse zooplankton community exists in Rijpfjorden during the midwinter, with a total of 49 zooplankton taxa being recorded in the samples collected using the two nets. Thus, the assemblage observed is richer concerning species diversity than if a single sampler had been used. For example only 42 taxa were collected in a seasonal study using just the MPS in the same region from March to October 2007 (Weydmann *et al*. 2013). Composition of the midwinter zooplankton community sampled by the MPS was dominated by *Pseudocalanus* spp. and *Oithona similis*, but *Calanus finmarchicus* and *C. glacialis* were also present in relatively large numbers; an observation similar to that reported by Weydmann *et al*. (2013) during autumn.

Only 16 of the total number of 49 zooplankton taxa sampled were common to both samplers; all of these were of intermediate size. So as expected, the small copepod species, gelatinous zooplankters and the young stages of pteropods and appendicularians were exclusively collected by the MPS; they would have been extruded through the large meshes of the MIK. Conversely, the large zooplankton, such as polychaetes, older stages of pteropods, appendicularians,

euphausiids, amphipods, and large gelatinous zooplankton were only taken by the bigger, more rapidly towed MIK net. The SIMPER analysis confirmed, there were distinct differences in the zooplankton community composition and structure sampled by the MPS net and the MIK net; the small copepod *O. similis*, which was not retained by the large mesh size of the MIK, contributed most to this differentiation.

Vertical distribution patterns in abundance and size of large zooplankters. — Large zooplankton such as euphausiids are fast swimmers (Vinogradov 1997) and may avoid small nets such as the MPS, which leads to considerable underestimation of the large size fraction when using standard mesozooplankton sampling gear (Sameoto *et al*. 2000). In this survey, by studying vertical distribution patterns using two contrasting gears, we have attempted to broaden the outlook for larger zooplankton community.

The two ctenophore species, *Beröe cucumis* and *Mertensia ovum*, were generally found at low abundance, which is in agreement with previous reports (*e.g*. Swanberg and Båmstedt 1991). Surprisingly high numbers of tiny *Beröe cucumis* were found only in the MPS samples (with a maximum abundance of 10 ind. m^{-3}), which is in accordance with Falkenhaug (1996) who observed very high biovolumes of this species in winter in northern Norway fjord. Otherwise, generally low abundances of gelatinous zooplankton we observed in MIK samples is consistent with the results of the seasonal study of macrozooplankton in Billefjorden, Svalbard (78°40'N) (Bandara *et al*. 2016), in which the vertical distributions of the larger (>1000 μm) zooplankton were assessed using vertical hauls (WP-3 net; 1000 μm mesh size) from three depth strata (0–50, 50–100 and 100–180 m) between August 2008 and May 2009. In interpreting the results of this study, it was assumed that both ctenophore species had descended to occupy deeper depths between August and October and then ascended back up to shallower depths from November. In Rijpfjorden our study shows that the abundance of *M. ovum* peaked at the intermediate depths (50–100 m depth layer in MPS samples and 75 m in MIK samples). Whereas the results of both nets showed that *B. cucumis* was concentrated at the surface 20 m. The autumn descent (and spring-summer ascend) is likely a response to the migrations of their prey (Bandara *et al*. 2016). *Mertensia ovum* feeds predominantly on *Calanus* spp., which during our Rijpfjorden study was also concentrated in the upper water column, whereas *B. cucumis* is a tertiary consumer that feeds specifically on *M. ovum* (Swanberg and Båmstedt 1991). So the vertical distributions of both species, which were revealed by both nets in our survey, may be a consequence of a typical prey-predator relationship as described in the Barents Sea by Swanberg and Båmstedt (1991). As expected, the observed size distributions of ctenophores in our survey varied with the samplers: *Mertensia ovum* had average lengths of 2.1 mm in MPS compared with 21.4 mm in the MIK samples. The size disparity

was even greater in *B. cucumis*, which had an average body size of 1.4 mm in MPS samples compared with 27 mm in MIK samples, but the maximum length values increased consequently towards the surface in both species and nets (Fig. 2a–b). Bandara *et al*. (2016), in their ten-month study in Billefjorden, reported that the populations of ctenophores were dominated by small specimens (mean annual body lengths were 6.7 mm for *M. ovum* and 2.9 mm for *B. cucumis*) but increased to 11 mm for *M. ovum* and 6 mm for *B. cucumis* in January 2009. In case of *M. ovum* the average value obtained in the same month as in our study in Billefjorden, is in agreement with our mean measurements from MPS and MIK, while it is much lower for *B. cucumis* sampled by MPS. It seems that the tiny but abundant population of *B. cucumis* was possible to be caught only by the net with the fine mesh size (*e.g*. MPS in our study), contrary to coarser WP-3 net used by Bandara *et al*. (2016). On the other hand, the size distributions of the last mentioned species inhabiting the northern Norway fjord (Falkenhaug 1996) demonstrated its size peak in winter (between 20 and 30 mm length), which seems to be in accordance with our MIK measurements (average 27 mm). The large disparity in average body size of ctenophores we sampled was undoubtedly the result of the different mesh sizes of the samplers, but the absence of larger individuals in MPS showed that MIK sampled larger individuals (>11 mm) much more efficiently in comparison with MPS. Our results on the abundance and length distribution of these organisms contribute on bridging gaps in the general knowledge of ctenophores distribution/sizes, but also emphasize the need to use at least two nets with different characteristics to properly examine these zooplankton assemblages.

Some authors have suggested that chaetognaths do not have a distinct seasonal distribution pattern (*e.g*. Hagen 1999). However, *Parasagitta elegans* peaked in abundance in summer and autumn in Billefjorden, Svalbard (Grigor *et al*. 2014). Chaetognaths are known to aggregate during winter in the hyperbenthic zone immediately above the seafloor (Choe and Deibel 2000), and Grigor *et al*. (2014) found all cohorts of *P. elegans* in deeper waters during winter. This suggests they undertake seasonal migration, possibly to track the distribution of overwintering copepods. Our study lends support to this hypothesis since we observed that the maximum abundances of both *Parasagitta elegans* and *Eukrohnia hamata* coincided with the surface concentrations of the herbivorous *Calanus* spp. in water column at 0–20 m in the MPS samples and at 75 m in the MIK samples. Two recent winter studies from the Arctic found low abundances of the chaetognaths both in Kongsfjorden – 0.3–1.1 ind. m^{-3} (Grenvald *et al*. 2016) and in Billefjorden – 2.4–14.7 ind. m^{-3} (Grigor *et al*. 2014), but these abundances were still higher than the ones we estimated in Rijpfjorden (0.3–1.2 ind. m^{-3} and 1.2–5.9 ind. m^{-3} in MPS and MIK samples, respectively). Similar patterns in the vertical distribution of *P. elegans* were reported in Billefjorfden in 2009 (Bandara *et al*. 2016) in which higher abundances were present both in the

deepest layers and near the surface – observations that are consistent with our MPS data. *Eukrohnia hamata* occurred in low abundances (0.02–0.35 ind. m^{-3} and 0.3–1.2 ind. m^{-3} in MPS and MIK samples, respectively) (Fig. 3b) and mainly in the upper layers (0–20 m in the MPS and at 75 m in the MIK); this is in accord with Richter (1995) who reported that this species inhabits the subsurface layer in the Greenland Sea for most of the year.

Our morphometric data for *P. elegans* (average lengths 22 mm in MPS and 23 mm in MIK net) are in good agreement with other polar night results (*e.g.* Grigor *et al*. 2014; Bandara *et al*. 2016), which indicated that around 80% of the population of the first year generation had a mean total length of 23.4 mm.

In Rijpfjorden in 2012 the euphausiids were mainly located in the upper waters but were caught in much larger numbers by the MIK than by the MPS; they are fast swimmers and so are able to avoid the smaller net. The most abundant euphausiid in our zooplankton material was the oceanic species *Thysanoessa longicaudata*. The coastal species *T. inermis* was also present and was the species dominating the macrozooplankton community in Kongsfjorden (Buchholz *et al*. 2010) where its high abundance (1.9–2.5 ind. m^{-3}) occurred in January 2014 (Grenvald *et al*. 2016). The third euphausiid species caught by MIK was a neritic species *T. raschii*, which occurred in relatively low abundances (maximum 0.06 ind. m^{-3}) similar to those reported in Kongsfjorden (Buchholz *et al*. 2010; Grenvald *et al*. 2016 and citations therein). The vertical distribution patterns of all three *Thysanoessa* spp. (our data) showed that the highest abundances occurred in the shallower water layers; this is consistent with the observation of Williams and Lindley (1982) who reported that between March and October in the North-eastern Atlantic a large population of *T. longicaudata* was concentrated in the upper 100 m. The clear pattern for the larger-sized euphausiids (all three species) to be deeper distributed in Rijpfjorden in January 2012 is consistent with the observations of Iguchi and Ikeda (2004) who reported a clear trend for larger specimens of *Thysanoessa longipes* to occur at deeper depths in the central Japan Sea. It was also confirmed in Kongsfjorden waters, that during polar night *T. inermis* and *T. raschii* overwinter in the deep and particularly so close to the sea bottom that a normally sampling zooplankton net could not reach them (Hirche *et al*. 2016), whereas the small half-yearlings individuals remained at the surface (F. Buchholz personal comm.). In Kongsfjorden, Grenvald *et al*. (2016) recorded the average length of *T. inermis* to be 12.2–12.8 mm in January 2014, whereas a broader range of sizes (10.3–16.7 mm) observed in Rijpfjorden in January 2012 might be the result of sampling three different depth layers (our study: 20 m; 75 m; 225 m) contrary to only one layer (Grenvald *et al*. 2016: 20 m).

This discrepancy might also suggest that both the knowledge on vertical distribution patterns and size structure of large zooplankters in various regions of Svalbard in midwinter is still scarce and need to be substantially supplemented.

The overwintering stages of *Calanus* spp. — Preliminary identification of the three *Calanus* species was conducted by using prosome length criteria (Kwasniewski *et al*. 2003) and such categorisation was used in general description of Rijpfjorden zooplankton community structure in the current study (Tables 3 and 4). In less than a decade, next-generation sequencing technologies have fundamentally changed our approach to the recognition of *Calanus* species. Gabrielsen *et al*. (2012) found out that the morphological identification of *Calanus* in Svalbard (also in Rijpfjorden) waters systematically overestimates the abundance of *C. finmarchicus* at the expense of *C. glacialis*, which inspired us to combine appropriate copepodite stages of two *C. finmarchicus* and *C. glacialis* into *Calanus* spp. when tracking their vertical distribution (Fig. 5). We share the opinion that such misidentification poses a serious problem in the use of these two species as indicators of Atlantic versus Arctic water masses and thus as climatic indicators.

Typically, populations of two smaller *Calanus* species, *C. finmarchicus* and *C. glacialis*, overwinter at greater depths than they inhabit during vegetation period either as adults or as late stage copepodites (*e.g*. Wold *et al*. 2011). It has been shown that large numbers of CIV and CV copepodids of both *C. finmarchicus* and *C. glacialis* were already present in surface waters in our study (Fig. 5a–b), which is similar to the midwinter observations of Berge *et al*. (2015) from the same region. Two recent seasonal studies by Lischka and Hagen (2016) and Bandara *et al*. (2016) have also described seasonal vertical patterns in abundance of *Calanus* age structure sampled by a modified Apstein closing net (100 µm mesh size, 0.2 m² mouth opening) and a larger WP3 net (mesh size of 1000 µm, 1 m² area of the opening) in Kongsfjorden and Billefjorden, respectively. Lischka and Hagen (2016) reported that in February 1999 the dominant stage was CV of *C. finmarchicus* (>50%), while stage CIV and females of *C. glacialis* (~30% each); these observations are similar to our results from MPS samples (data not shown: CV of *C. finmarchicus* – 57%; CIV and females of *C. glacialis* – 54% and 9%, respectively).

Calanus spp. males, which are usually rare in typical mesozooplankton samples, were present mainly in November 1998 and February 1999 in the two deeper layers (>50 m) with the peak below 100 m depth in Kongsfjorden (Lischka and Hagen 2016). In comparable month with our study Bandara *et al*. (2016) reported that males of the two smaller *Calanus* species were distributed mostly in the upper 50 m of Billefjorden, which is similar to our observations (0–20 m) from Rijpfjorden (Fig. 5d).

The copepodite stages CIII and CIV of *C. hyperboreus* occurred almost exclusively in the MPS samples, whereas CV and adult females dominated the population in the MIK assemblage (our study; Fig. 6b), Although we are aware that partly responsible for the disproportion in numbers of older *Calanus* copepodites between both nets could be also the big difference in volume of

filtered seawater by the two nets (the average 13 m^3 for MPS vs. 4161 m^3 for MIK), the comparison of the large MIK net in relation to small MPS results demonstrates very well supplementary role of both vertical distribution patterns.

In January 1999 the dominant CIV stage of *C. hyperboreus* was concentrated at the deepest sampled layer (>100 m) in Kongsfjorden (Lischka and Hagen 2016), which is in accordance with our data from both samplers.

Sampling considerations. — The mathematical model for assessing the selectivity of high-speed plankton nets in North Sea zooplankton developed by Nichols and Thompson (1991) estimated that ~95% of copepods with a carapace width ≥ 75% of the sampler's mesh size are efficiently retained by a net. Gallienne and Robins (2001) also stated that the carapace width of the smallest target organism efficiently retained by mesh of a given size would be 75% of that mesh size. So it seems that the rule also applies to the more slowly hauled nets, as used in our survey (as well as in the other surveys mentioned above). When interpreting our detailed *Calanus* morphometric data (lengths and widths) it should be born in mind that 1125 μm is 75% of the MIK mesh size. Thus only the older, larger-sized specimens will be efficiently retained by the larger net, i.e. only adults of *C. glacialis*, and late copepodite stages CIV-CV and adults of *C. hyperboreus* (Table 4).

Hence, our MIK data provide noteworthy supplementary information about the distributions, age structures and sizes of adults of two larger *Calanus* species, which are seldom taken in adequate numbers in mesozooplankton samplers such as the MPS. However, theoretically none of stages of *C. finmarchicus* have prosome widths broad enough to be retained effectively by the MIK net with 1500 μm that we used. Bandara *et al.* (2016) also found that in Kongsfjorden only the older copepodites (with width >750 μm) were taken representatively by their 1000 μm mesh size sampler.

Summary. — Obtaining accurate estimates of a broad size spectrum of zooplankton species is important because data on diversity and abundances is the fundamental in order to understand ecological processes (*e.g.* estimation of carbon fluxes). The recent paper on plankton patchiness (Trudnowska *et al.* 2016) based on a laser optical plankton counter (LOPC), a fluorometer and CTD measurements (along several sections in the surface 50 m of the West Spitsbergen region with additional data from zooplankton net sampling and hydrographical measurements at stations), observed that zooplankton patches, which differed in terms of size, number and distribution patterns, occupied only a minor portion of the studied ocean area (2–17%). It was also found in this study that two smaller (small and medium) zooplankton fractions distributions were sensitive to increased primary production, optimal hydrography, discontinuities in the density field and/or the presence of meanders/eddies, while large copepods size fraction (L: 0.8–5.0 mm Equivalent Spherical Diameter) were independent of

any oceanographic feature, which pointed towards biological cues (*e.g.* seasonal and ontogenetic migration, food availability and predatory risk) as main factors regulating aggregation processes of macrozooplankton. Thus, in our study we have shown that horizontal plankton tows sampling much larger volumes of seawater (MIK) provide important, supplementary information on bigger zooplankton community structure in terms of age structure, abundance and sizes to those obtained from vertical MPS hauls. Combining data from these two samplers gave substantially higher estimates of the species diversity (49 taxa) than those based on the individual samplers (MPS: 38 taxa, MIK: 28). This is especially important in the context of the limited knowledge and accessibility to the midwinter zooplankton community in the high Arctic regions.

Additionally, our data demonstrated how much the large MIK net was more effective in sampling older stages (CIV-CVI, >1125 μm) of larger *Calanus* species than the smaller MPS (the same would apply to other mesozooplankton samplers such as the WP2 and WP3 with fine mesh). The youngest stage present (CIII) of *Calanus* spp. was sampled exclusively by the MPS, and the share of CIV copepodites in MPS was double that than in MIK samples. In contrast, catches of the CV-CVI copepodites of *Calanus* spp. were substantially higher in the MIK samples (3-fold and 5-fold higher for adult males and females, respectively). Analogous comparison for *C. hyperboreus* gave even more striking result; almost 5-fold and 10-fold higher share of CV copepodites and adults females in MIK than MPS samples, respectively. Moreover, in the MIK samples greater numbers of all three *Thysanoessa* species occurred predominantly in the upper layers, but there was a clear tendency for the larger-sized euphausiids to occur deeper.

Consistent patterns for the vertical distributions of the large zooplankters (*e.g.* ctenophores) collected by the two gears provided far better data on their abundances and sizes than obtained by the samplers usually used (*e.g.* MPS). Additionally our results from both nets demonstrated that there were high abundances of *Calanus* spp. and their predators (ctenophores and chaetognaths) in the upper water layers.

This study has provided an initial snap-shot of how combined zooplankton sampling with two samplers with different characteristics (MPS and MIK) can deliver useful additional insights into the composition and size structure of zooplankton communities not only in the polar seas but elsewhere. By examining with special caution large zooplankters, our midwinter study delivered valuable knowledge on patchy and rare distributed animals (*e.g.* euphausiids or ctenophores), which provide a means of linking the structure of the zooplankton assemblages with that of the micronekton.

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